

Gender-Related Factors Affecting Primate Social Behavior: Grooming, Rank, Age, and Kinship in Heterosexual and All-Male Groups of Stumptail Macaques

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ABSTRACT The structure of grooming relations was studied in three captive groups of stumptail macaques, two heterosexual (consisting mainly of females) and one all male. Compared to the heterosexual groups, social hierarchy in the all-male group was less linear, and agonistic and peaceful activity of low-ranking individuals toward high-ranking ones was higher. In addition, in the all-male group received grooming was more variable than performed grooming and showed stronger dependence on age. No effect of maternal kinship was found in the all-male group, and individual preferences were also less marked in this group than in heterosexual groups. These differences tend to be related to dominance style and dispersal patterns.

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All aspects of primate behavior (social, exploratory, manipulatory, sexual, and parental) are sex dimorphic (Boesch and Boesch, 1981; Fedigan and Baxter, 1984; Medicus and Hopf, 1990). This is true even of feeding (Cords, 1986) and predator avoidance (van Schaik and van Noordwijk, 1989). However, the effect of genetic factors underlying sex-specific and species-specific predisposition to certain behavioral strategies may be modified by the male-female ratio in the group. To reveal this predisposition, one should examine groups belonging to one species, kept under identical conditions, but differing in sex ratio. This is the general design of our study.

Stumptail macaques (*Macaca arctoides*) were chosen for investigation. This species is known for its relaxed and egalitarian dominance style, which is characterized by such features as a low level of severe aggression, strong tendency for reconciliation, affiliation, and tolerance toward subordinates (de Waal and Ren, 1988; de Waal, 1989; de Waal and Luttrell, 1989; Caldecott, 1986; Butov-

skaya, 1987, 1993, 1994; Butovskaya and Ladygina, 1989; Butovskaya and Kozintsev, 1994; Butovskaya et al., 1994). In this respect, stumptails resemble tonkeana macaques and possibly also bonnets and Barbary macaques, but provide a sharp contrast with "despotic" macaque species like rhesus and perhaps pigtail and Japanese monkeys (Shively et al., 1982; Caldecott, 1986; Thierry, 1985, 1990; de Waal and Luttrell, 1989; Moore, 1992).

Grooming was selected as the principal behavioral parameter. Besides having a purely hygienic function, grooming is one of the main forms of affiliative behavior, a means of establishing and restoring friendly bonds, reducing tension, and preventing aggression (Carpenter, 1964; Hausfater and Sutherland, 1984; Easley et al., 1989; Thierry et al., 1990).

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In most studies on stumptails, grooming was found to be influenced by dominance status, especially in females, who are generally more inclined to grooming than are males (Estrada et al., 1977; O'Keefe et al., 1982; Nieuwenhuijsen et al., 1988; Lopez-Vergara et al., 1989; Thierry et al., 1990; Butovskaya and Kozintsev, 1994; Butovskaya et al., 1994). According to Seyfarth's model, based on other cercopithecine species, high-ranking females should be groomed most frequently, and grooming should usually occur among females who are close to each other in rank (Seyfarth, 1977, 1983). According to Silk's "extortion hypothesis," high-ranking females should not only receive the largest share of grooming, but should also be able to afford to groom their subordinates less often (Silk, 1982). However, in some studies on stumptails the effect of dominance on grooming was not detected (Thierry et al., 1990).

This study focuses on the effect of two gender-related factors, including (1) gender itself and (2) sex ratio, on grooming behavior and its interrelationship with dominance and other factors. An ideal design for such a study would be first to compare an all-male group with an all-female one. The former was available to us, but the latter was not and will probably never be (see Discussion). Instead, we had to compare an all-male group with two heterosexual groups in which the proportion of females was much higher than the one observed in natural populations.

Although the number of females per male in free-ranging stumptails is not known, in nine other macaque species it ranges from one to eight. Barbary and bonnet macaques (species supposedly similar to stumptails in "dominance style") are close to the lower limit, apparently due to low male emigration rates (Caldecott, 1986). How would females behave if they outnumbered males by a factor of 10 or even 20? What would males do if they were outnumbered in such a proportion? And, conversely, what would they do without females? These are the questions addressed in this study.

MATERIALS AND METHODS

Three groups of stumptail macaques were observed at Sukhumi Primate Research

TABLE 1. Sex and age composition of the groups

Group	Adults		Juveniles		Infants		Total
	♂♂	♀♀	♂♂	♀♀	♂♂	♀♀	
H1	1	17	7	11	1	1	38
H2	2	17	6	10	—	1	36
M	11	—	—	—	—	—	11

Center, Republic of Georgia, during the summer and autumn of 1986–1988. Two of the groups, H1 and H2, were heterosexual, each consisting mainly of females and a leading male (in H2 the second, low-ranking male was also present), and one group M, was all male (Butovskaya and Ladygina, 1989; Butovskaya and Kozintsev, 1994; Butovskaya et al., 1994). The monkeys were kept in large outdoor corrals with indoor sections for sleep and feeding. Information on sex and age structure of the groups is given in Table 1. All animals were individually identified and their maternal kinship relationships were known.

Observations were made using the focal-animal sampling method (Altmann, 1974). In groups H1 and M, 10 30 min samples were collected per adult individual. In group H2, the number of samples was larger and differed between individuals, so the frequencies were adjusted per 10 samples. Sociometrical matrices were constructed, and their symmetrical elements were compared by means of the binomial test. For each animal, a dominance index (Zumpe and Michael, 1986) was calculated on the basis of aggression, ritualized biting, grinning, and presenting behavior. For the sake of convenience, the continuous distribution range of the index was divided into three nearly equal classes (high, medium, and low). The degree of linearity of hierarchy was assessed for the entire group. Because some animals had never demonstrated dominance or submission to each other, we have generalized Landau's index of linearity (Lehner, 1979) in the following way:

$$h^* = \frac{3}{n} \frac{n-1}{n+1} \sum_{i=1}^n \frac{(2a_i - b_i)^2}{b_i},$$

in which a_i represents the number of the i th individual's "subordinates" (as in the dominance index, this quantity may be fractional

in some dyads if each of the two partners had dominated at least once), b_i is the number of individuals with which the i th individual had had dominance/submission interactions, and n is group size. If each animal had had at least one such interaction with each of the remaining animals ($b_i = n - 1$ in each case), the formula reduces itself to Landau's index.

The minimum level of significance in all statistical tests undertaken in this study is the 0.05 level. To test the hypothesis that no individual variation existed either in performed or in received grooming, the coefficient of dispersal, CD (variance divided by the mean), was calculated for each frequency distribution. The significance of deviation from the Poisson (random) distribution was tested using the formula $\chi^2 = CD (n - 1)$, and the resulting values were compared with points of the χ^2 distribution with $n - 1$ degrees of freedom. To test the hypothesis that no individual preferences existed, the expected values of elements of the grooming matrix were estimated using Wagner's iterative algorithm (Wagner, 1970), and the χ^2 test with $n(n - 3) + 1$ degrees of freedom was applied. On its basis, Tchuproff's T-coefficient of contingency was calculated (Apton, 1978).

Association between grooming and other variables was examined both at the level of overall individual characteristics (using correlation coefficients, which were subjected to principal component analysis) and at the level of dyadic interactions (using permutation tests). In the latter case, correlation was estimated between the rows and columns of the two matrices separately (Hemelrijk, 1990). With one asymmetrical matrix (for instance, that of grooming), correlation is tested between the original matrix and its transpose, the result showing the degree of reciprocity. With two asymmetrical matrices (for instance, those of grooming and dominance), there are four possible combinations. Thus, a positive correlation between the columns of the first matrix and the rows of the second would mean that performed grooming is correlated with submission (animals which groom animal X more often than others do are more likely than are others to be "defeated" by this animal). Elements of the matrices were ranked within each row

and column separately, the crossproduct was calculated, and the significance level was set at L/T if $L > S$, $(L + E)/T$ if $L < S$, or 0.5 if $L = S$. L , S , and E are the number of permutations in which the crossproduct was larger than, smaller than, or equal to the original value, respectively, and T is the total number of permutations (1,000 in each case). To use this test for evaluating the effect of maternal kinship, each dyad was given the value of 1 if its members belonged to the same matriline, or zero otherwise.

To test the "extortion hypothesis," coefficients of grooming status of the i th animal against the j th were calculated for each dyad as $s_{ij} = g_{ij}/(g_{ij} + g_{ji})$. g_{ij} is the number of times when the i th animal groomed the j th, and g_{ji} the number of times when the roles were reversed. Then the overall grooming status was calculated for each animal by averaging s_{ij} over all the i th animal's partners (Butovskaya et al., 1994).

To investigate the structure of grooming relations, pairwise grooming distances were calculated using the formula $d_{ij} = 1 - n_{ij}/n_{\max}$; n_{ij} is the total number of grooming contacts between the i th and j th individuals, and n_{\max} the maximal number of such contacts between two individuals in the group. Raw d_{ij} values were subjected to cluster analysis, and logarithmically transformed d_{ij} values to nonmetrical multidimensional scaling (Easley et al., 1990; Butovskaya and Kozintsev, 1994; Butovskaya et al., 1994).

Each of the bisexual groups was analyzed in two ways. First, all dyadic interactions were considered, and then those between females only. Clearly, in the latter case, the "exclusion" of males is just a mental act which makes it possible to see how females behave in the presence of males, *not* in their absence.

RESULTS AND DISCUSSION

Findings on the Sukhumi stump-tail macaques

The linearity index equals 0.88 in group H1, 0.84 in group H2, (0.88 and 0.78, respectively, if only relationships between females are considered), but only 0.62 in group M. So the hierarchy was the least rigid in the male group. The average individual frequency of agonistic contacts was twice as

high in the all-male group as it was in the heterosexual groups (34.2 vs. 16.1–17.5 and 13.0–13.2 for females alone).

Individual variation in agonistic and grooming behavior. Individual and rank-related variation in agonistic actions in groups H1, H2, and M are shown graphically in Figures 1 and 2. Individuals in group M differed not so much in the number of "victories" (even the lowest-ranking male had had eight of them, while some females in groups H1 and H2 had "won" only once or even never) as in the number of "defeats," which ranged from 2 to 31 vs. 0–21 in groups H1 and H2 (1–17 for females). The coefficient of dispersal (Fig. 1) of the number of "victories" is minimal (4.4 vs. 9.9–10.5 in groups H1 and H2; females, 5.3–6.4). The number of "defeats" shows the reverse order of CD values: 5.7 vs. 3.5–3.7; females, 2.5–3.8. The explanation of these findings is given in Figure 2. In the male group, in contrast to the heterosexual groups, low-ranking individuals did not avoid agonistic contacts. While in groups H1 and H2 an average low-ranking individual was engaged in 11.7 such contacts, and an average high-ranking animal in almost twice as many (21.5; females alone, 10.7 vs. 17.1), the respective

frequencies in group M are almost equal: 35.0 and 32.7 (Fig. 2). Moreover, the subordinate males in group M sometimes won victories, even when their partners were dominants. Thus, the male F-1, whose dominance index is 0.24, beat the male B-2 (dominance index, 0.61) in four bouts out of seven. Such marked loops in the social hierarchy were not observed in heterosexual groups. The number of aggression cases per individual was almost the same in all groups (H1, 16.8; H2, 19.8; females, 14.4–14.7, vs. 16.0 in M), but the ratio of contact to noncontact aggression was minimal in the male group.

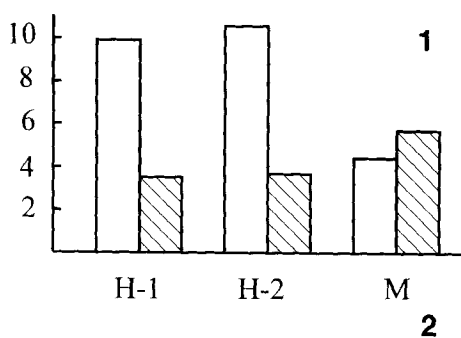
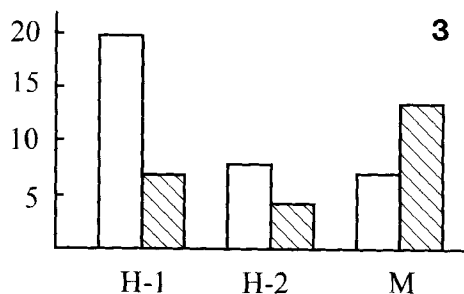
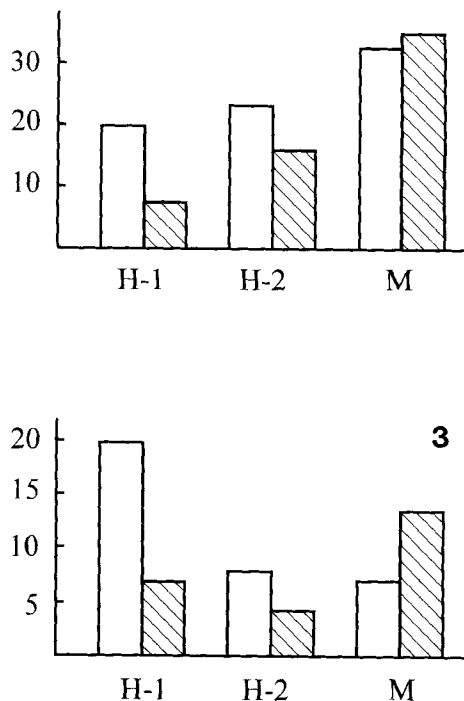


Fig. 1. Coefficient of dispersal (CD) of the number of "victories" (plain bars) and "defeats" (hatched bars) in agonistic interactions. H1 and H2 are heterosexual groups; M is all male. In the all-male group, the number of "victories" shows less individual variation than in the heterosexual groups. The situation is reversed with the number of "defeats." See text for other comments.

Fig. 2. Frequency of agonistic interactions per individual: high ranking (plain bars) and low ranking (hatched bars). H1 and H2 are heterosexual groups; M is all male. In the heterosexual groups, high-ranking individuals had had significantly more agonistic interactions than had the low-ranking ones. In the all-male group, the frequency of agonistic interactions was significantly higher than in the heterosexual groups, and showed no dependence on rank. See text for other comments.

Fig. 3. Coefficient of dispersal of the number of grooming contacts: active (plain bars) and passive (hatched bars). H1 and H2 are heterosexual groups; M is all male. In the all-male group, the frequency of active grooming contacts shows less individual variation than in the heterosexual groups. The situation is reversed with the frequency of passive grooming contacts. See text for other comments.



As Tables 2–4 indicate, grooming intensity was similar in all groups (30–39 active and passive contacts per individual in groups H1 and H2, including 26–32 female–female contacts on average, vs. 33 in group M). The number of grooming partners per individual in the all-male group was absolutely smaller than in the heterosexual groups, but relative to their possible number it was larger, evidently due to the smaller size of the male group. In this group, the indicators of performed grooming (frequency of active contacts and number of passive partners) have the lowest coefficients of dispersal, while the CD value for the number of passive contacts is the highest (Fig. 3). Group M is the only one in which the variation of the frequency of passive contacts is higher than that of the active contacts, implying that here, in contrast to the bisexual groups, and to females in particular, the attractiveness of an individual as a grooming partner was a more important individual characteristic than was its grooming performance. (As the CD values demonstrate, the number of partners is a less sensitive measure in this case than is the grooming frequency.)

Association between grooming and dominance, age, and maternal kinship. As seen from Table 5 and from Table 6 derived from it, the structure of correlations in the three groups shows both similarities and differences. The first general tendency is the positive correlation between received grooming (frequency of passive contacts, number of active partners) and dominance status (Table 5). In all the three groups, this tendency is reflected by the first principal component (PC1) (Table 6). Formally, however, the dominance index is directly related with received grooming only in group H1 (although its correlation with measures of received grooming is below significance level here and almost disappears when the male is “excluded”) (Table 5). In two other groups, the dominance index shows positive association with age. Strangely enough, this is true even when only interactions between females in group H2 are considered ($r = 0.47$, $P < 0.05$), although generally age is known to have little if any effect on female rank. Age is the only independent variable in our

analysis, and when it is held constant, the partial correlation coefficient of PC1 with dominance index is only 0.27 in group H2 (females, 0.04) and 0.46 in group M, vs. 0.75 in group H1 (females, 0.59). It would probably be premature to conclude that age per se may define the amount of received grooming. More likely, age may sometimes be a better predictor of true social status in males than is the dominance index, especially when the latter is based on an insufficient number of observations and the hierarchy is not very linear.

The second general tendency, positive correlation between performed and received grooming, is much more evident in Table 7, in which each pairwise interaction is taken into account, than in Tables 2–5, in which these interactions are summed over all the partners of an individual. The difference means that the principal factor underlying the association between performed and received grooming is reciprocity, which acts mainly at the dyadic rather than at the individual level.

Although the tendency of adjacently ranked animals to form stable grooming dyads is significant only in females of group H1 (Table 7), the alpha males in all three groups maintained closer affiliative relations with high-ranking individuals than with low-ranking ones (Tables 8–10). The same applies to high-ranking females in groups H1 and H2.

Table 7 also shows that in both heterosexual groups, grooming between maternal relatives was significantly more frequent than between those belonging to different matriline; in group H1, this tendency becomes less apparent when the male is excluded.

In several respects, the two heterosexual groups were different. In group H1, performed grooming shows an even stronger positive correlation with dominance index and PC1 (Table 6) than does received grooming (both are virtually independent of age). This defined the special role of the alpha male C-1, who shows maximal values of all the respective variables. His activity was directed mostly at high-ranking and medium-ranking females (Table 8). When only relationships between females are considered, the association between performed grooming

TABLE 2. Parameters of grooming behavior for group H1

Individual code ¹	Age, years	Dominance index	Frequency of contacts		Number of partners			Grooming status
			Active	Passive	Active	Passive	Two way	
C-1	7	1.00	106	63	10	16	10	0.24
A-1	13	0.87	45	38	8	9	6	0.44
I-1	11	0.82	49	38	11	11	8	0.45
E-1	16.5	0.67	23	26	6	8	4	0.44
G-1	>13	0.63	17	18	6	7	4	0.46
C-2	9	0.58	45	79	10	6	4	0.72
K-1	6.5	0.58	30	56	11	6	5	0.70
H-1	10	0.53	101	42	7	15	6	0.19
D-1	18.5	0.53	40	39	8	7	5	0.52
L-1	5	0.46	19	25	9	10	5	0.50
B-1	10.5	0.35	26	44	10	9	5	0.57
A-2	10	0.32	24	58	13	9	8	0.73
B-4	9	0.25	73	34	6	13	5	0.20
D-3	4	0.25	44	39	10	12	7	0.46
F-2	5	0.13	5	24	9	2	1	0.87
I	8	0.00	28	19	6	3	2	0.68
F-1	>15	0.00	39	46	7	6	4	0.53
J-1	8	0.00	21	37	8	7	5	0.62
G-2	3.8	0.00	7	17	6	5	3	0.61
\bar{x}	—	—	39.1 (31.8)	39.1 (31.8)	8.5 (7.5)	8.5 (7.5)	5.1 (4.2)	—
s	—	—	27.8 (20.2)	16.4 (13.0)	2.1 (2.0)	3.7 (3.1)	2.1 (1.7)	—
CD	—	—	19.8 (12.8)	6.9 (5.3)	0.5 (0.5)	1.6 (1.3)	0.9 (0.7)	—
χ^2	—	—	356.6** (217.0**)	124.3** (89.9**)	9.3 (9.1)	29.6* (21.4)	16.0 (11.2)	—

¹C-1 is a male, others are females. Members of a matriline are denoted by the same letter. \bar{x} , mean; s, standard deviation; CD, coefficient of dispersal; χ^2 , value of the chi-squared test. Figures in parentheses refer to females. See Butovskaya et al. (1994) for the grooming matrix.

* $P < 0.05$.

** $P < 0.001$.

and dominance index becomes insignificant. High-ranking and medium-ranking females were most interested in grooming the male, from whom they received much in exchange. The minimal values of PC1 are found in the youngest female G-2 and other low-ranking animals, who declined to enter into active grooming relations and were the least attractive partners for other group members. PC2 (Table 6) describes the decrease of received grooming with age in some animals. Also, the age difference between grooming partners in group H1 is significantly below average (Table 7).

In group H2, performed grooming, unlike received grooming, is not correlated with the dominance index at the individual level, although at the level of pairwise interactions (Table 7) its positive correlation with dominance becomes evident, as in group H1. Also, performed grooming in group H2 shows a significant decrease with age (this is even more evident if females alone are considered); both its measures have negative load-

ings on PC1 (Table 6). For the alpha male, as for his counterpart in group H1, the high-ranking females were the preferred partners (Table 9). However, he was much less active and did not differ from the females in any of the grooming measures. Neither did the young low-ranking male N-1; yet he was very active in grooming the alpha male and especially the old female R-1, whose rank was much higher than his and who showed much reciprocity toward him. The high-ranking females preferred to groom the alpha male and were least interested in low-ranking females. In other respects, females of different categories were rather similar. The top places on PC1 are taken by the alpha female U-1, who was the favorite partner of groomers, and T-1, a medium-ranking female, the oldest in the group, whose grooming performance was close to minimal. On the opposite end of PC1 scale is female 3, who is close to T-1 in rank but much younger; her characteristics of performed grooming were maximal, and those of received grooming low. PC2 in

TABLE 3. Parameters of grooming behavior for group H2

Individual code ¹	Age, years	Dominance index	Frequency of contacts		Number of partners			Grooming status
			Active	Passive	Active	Passive	Two way	
1	12	0.93	31.9	45.4	11	15	10	0.46
N-1	4	0.21	35.6	27.1	5	13	3	0.23
U-1	>11	0.87	31.4	56.7	17	14	12	0.60
W-1	6.5	0.80	29.0	32.6	12	12	7	0.51
Q-1	>14	0.77	34.2	34.3	11	6	4	0.66
T-1	>18	0.68	11.2	35.9	10	6	3	0.72
R-1	>13	0.67	40.7	19.5	5	11	3	0.21
3	6	0.66	82.3	15.5	7	16	5	0.18
O-1	>15	0.62	23.7	42.4	13	11	7	0.61
M-1	19	0.60	4.3	25.0	9	3	3	0.91
P-1	10	0.53	17.7	24.6	10	7	6	0.61
2	10	0.52	17.7	38.4	14	4	3	0.81
O-3	5.5	0.43	28.9	19.7	6	12	4	0.29
N-2	9.5	0.42	23.4	33.4	11	9	6	0.57
V-1	9.5	0.32	36.1	19.4	7	12	4	0.33
4	5	0.21	39.5	24.2	13	15	9	0.42
S-1	>12	0.20	28.0	43.9	14	9	6	0.66
X-1	6.5	0.20	35.1	30.9	15	11	9	0.62
S-2	3	0.16	24.7	19.5	5	6	1	0.44
M-3	11.5	0.11	18.5	11.1	8	9	4	0.41
N-3	3.5	0.09	37.5	31.8	9	11	7	0.41
\bar{x}	—	—	30.1 (26.3)	30.1 (26.3)	10.1 (8.9)	10.1 (8.9)	5.5 (4.8)	—
s	—	—	15.3 (16.1)	11.3 (12.6)	3.5 (3.3)	3.7 (3.7)	2.8 (2.7)	—
CD	—	—	7.8 (9.9)	4.2 (6.1)	1.2 (1.2)	1.3 (1.6)	1.4 (1.5)	—
χ^2	—	—	155.6* (178.7*)	84.6* (109.0*)	24.3 (21.6)	26.9 (28.3)	28.1 (26.1)	—

¹1 and N-1 are male, others are females. Frequencies are adjusted per 10 samples. Figures in parentheses refer to females.* $P < 0.001$.

TABLE 4. Parameters of grooming behavior for group M

Individual code ¹	Age, years	Dominance index	Frequency of contacts		Number of partners			Grooming status
			Active	Passive	Active	Passive	Two way	
B-1	11	0.95	60	58	9	9	8	0.47
A-1	14	0.81	19	48	8	2	2	0.89
K-1	12	0.73	24	28	7	9	7	0.40
B-2	10	0.61	37	28	8	6	6	0.59
Q-1	7	0.52	13	17	6	5	4	0.62
E-1	9	0.50	26	25	7	8	6	0.51
C-1	11	0.38	51	81	8	7	6	0.56
F-2	7	0.35	54	21	5	6	3	0.38
F-1	8	0.24	28	18	7	9	7	0.36
C-2	7	0.23	31	8	3	7	2	0.23
J-1	7	0.14	24	35	5	5	3	0.54
\bar{x}	—	—	33.4	33.4	6.6	6.6	4.9	—
s	—	—	15.3	21.3	1.7	2.2	2.2	—
CD	—	—	7.0	13.5	0.5	0.7	1.0	—
χ^2	—	—	70.3* (178.7*)	135.5* (109.0*)	4.6 (21.6)	7.0 (28.3)	9.6 (26.1)	—

¹All animals are males. See Butovskaya and Kozintsev (1994) for the grooming matrix.* $P < 0.001$.

this group shows little dependence on either age or dominance index.

The male group differs from the heterosexual groups in several respects. First, groom-

ing activity here was directed mostly up the social hierarchy and distributed in a step-wise fashion: the low-ranking individuals had the largest number of active contacts

TABLE 5. Correlation coefficients between grooming measures, age, and dominance index¹

Variables	Group H1	Group H2	Group M
Age vs. dominance index	0.28 (0.41)	0.52* (0.47*)	0.76**
Frequency of active contacts vs. freq. of passive contacts	0.46* (0.19)	-0.22 (-0.21)	0.49
Number of active partners vs. number of passive partners	0.18 (0.06)	0.01 (-0.02)	0.12
Frequency of active contacts vs. age	0.06 (0.21)	-0.47* (-0.48*)	0.05
Frequency of passive contacts vs. age	0.03 (0.14)	0.33 (0.31)	0.61*
Number of active partners vs. age	-0.26 (-0.24)	0.24 (0.21)	0.74**
Number of passive partners vs. age	-0.03 (0.04)	-0.45* (-0.52*)	-0.13
Frequency of active contacts vs. dominance index	0.48* (0.21)	0.03 (0.00)	0.14
Frequency of passive contacts vs. dominance index	0.36 (0.15)	0.45* (0.24)	0.36
Number of active partners vs. dominance index	0.29 (0.23)	0.24 (0.15)	0.72*
Number of passive partners vs. dominance index	0.52* (0.36)	0.07 (0.01)	0.00
Coefficient of grooming status vs. age	-0.21 (-0.27)	0.59** (0.59**)	0.57
Coefficient of grooming status vs. dominance index	-0.44 (-0.26)	0.21 (0.17)	0.44

¹ Figures in parentheses refer to females.

* $P < 0.05$.

** $P < 0.01$.

TABLE 6. Correlation coefficients between age, behavioral variables, and the first two principal components (PCs)¹

Variable	Group H1		Group H2		Group M	
	PC1	PC2	PC1	PC2	PC1	PC2
Age	0.07 (0.44)	0.65 (0.25)	0.79 (0.78)	-0.19 (-0.21)	0.88	-0.32
Dominance index	0.74 (0.66)	0.23 (-0.12)	0.55 (0.39)	0.44 (0.26)	0.81	-0.21
Frequency of active grooming contacts	0.82 (0.80)	0.33 (0.34)	-0.64 (-0.72)	0.63 (0.50)	0.39	0.78
Frequency of passive grooming contacts	0.73 (0.41)	-0.42 (-0.74)	-0.74 (0.69)	0.52 (0.61)	0.79	0.15
Number of active grooming partners	0.50 (0.18)	-0.77 (-0.92)	0.65 (0.61)	0.47 (0.67)	0.91	0.00
Number of passive grooming partners	0.81 (0.81)	0.25 (0.25)	-0.48 (-0.66)	0.79 (0.63)	0.05	0.79
Share in the total variance, percent	44.5 (35.3)	23.7 (27.2)	42.3 (42.7)	29.1 (26.4)	50.8	23.5

¹ Figures in parentheses refer to females. PC1 in group H1 indicates that the association of high dominance index and grooming, both performed (active grooming contacts + passive grooming partners) and received (passive grooming contacts + active grooming partners), has little relationship to age, in contrast to the situation in groups H2 and M. See text for other comments.

with the middle-ranking animals, the latter with the high-ranking ones, and the high-rankers with members of their own category, the alpha male being the animal with the maximal number of active partners (Tables 4, 10). This stepwise pattern is not seen in either of the heterosexual groups, where low-ranking females did not display any increase

of grooming activity toward animals of a higher social position (Tables 8, 9).

Second, the positive correlation between the dominance index and age in the male group is the strongest. This should be expected, since male status normally increases up to a certain age, and none of the males were very old. Both measures of received

TABLE 7. Probabilities of random correlation between matrices obtained by permutation tests¹

Variables	Group H1	Group H2	Group M
Performed grooming vs. received grooming	0.000*** (0.000***)	0.000*** (0.001**)	0.000***
Performed grooming vs. dominance	0.009** (0.051)	0.017* (0.026*)	0.056
Received grooming vs. dominance	0.064 (0.133)	0.065 (0.102)	0.007**
Performed grooming vs. submission	0.558 (0.344)	0.292 (0.279)	0.114
Received grooming vs. submission	0.068 (0.048*)	0.104 (0.100)	0.796
Performed grooming vs. difference in dominance index	0.741 (0.894)	0.833 (0.770)	0.913
Received grooming vs. difference in dominance index	0.925 (0.934)	0.872 (0.786)	0.829
Total grooming vs. difference in dominance index	0.902 (0.958*)	0.838 (0.650)	0.849
Performed grooming vs. difference in age	0.972* (0.983*)	0.829 (0.689)	0.847
Received grooming vs. difference in age	0.960* (0.977*)	0.631 (0.497)	0.409
Total grooming vs. difference in age	0.992** (0.997**)	0.765 (0.556)	0.761
Performed grooming vs. maternal relatedness	0.030* (0.079)	0.009** (0.003**)	0.177
Received grooming vs. maternal relatedness	0.013* (0.046*)	0.023* (0.001**)	0.471
Total grooming vs. maternal relatedness	0.043* (0.098)	0.015* (0.002**)	0.248

¹ Figures in parentheses refer to females. Probabilities below 0.5 imply a positive correlation, those above 0.5, negative (see text for explanations).* $P < 0.05$ or $P > 0.95$.** $P < 0.01$ or $P > 0.99$.*** $P < 0.001$ or $P > 0.999$.

TABLE 8. Mean frequency of grooming contacts per partner (actual or potential), according to sex and dominance status in group H1

Individuals ¹	Male	Females I	Females II	Females III	Average
Male	—	7.67	7.40	3.29	5.89
Females I	5.50	1.93	2.20	1.24	1.94
Females II	4.80	2.40	2.70	1.71	2.33
Females III	0.86	1.88	1.46	1.93	1.72
Average	3.50	2.36	2.31	1.71	2.17

¹ Rows show active contacts; columns show passive contacts. Status categories: I = high; II = medium; III = low.

TABLE 9. Mean frequency of grooming contacts per partner (actual or potential), according to sex and dominance status in group H2

Individuals ¹	Alpha male (1)	Male N-1	Females I	Females II	Females III	Average
Alpha male (1)	—	1.33	3.01	0.69	1.28	1.59
Male N-1	6.67	—	3.46	0.34	0.97	1.78
Females I	4.01	2.40	2.03	2.19	1.03	1.91
Females II	1.14	0.11	1.38	0.69	1.33	1.08
Females III	1.11	1.78	1.01	1.78	1.83	1.53
Average	2.27	1.36	1.62	1.45	1.34	1.50

¹ Rows show active contacts; columns show passive contacts. Status categories: I = high; II = medium; III = low.

TABLE 10. Mean frequency of grooming contacts per partner (actual or potential), according to dominance status in group M

Individuals ¹	Alpha male (B-1)	Other males I	Males II	Males III	Average
Alpha male (B-1)	—	7.67	9.67	2.00	6.00
Other males I	10.33	3.83	1.44	1.08	2.67
Males II	5.67	2.89	2.33	2.75	3.00
Males III	2.50	2.67	5.58	2.33	3.43
Average	5.80	3.47	4.10	2.05	3.34

¹ Rows show active contacts; columns show passive contacts. Status categories: I = high; II = medium; III = low.

grooming, too, show a significant positive correlation with age, and the number of active partners is also correlated with the dominance index. Overall, all four variables have the highest loadings on PC1 (Table 6), whose share in the total variation is maximal here. One extreme of the PC1 scale is occupied by the leader B-1, who was groomed by all group members except one. On the opposite extreme is a young low-ranking male, C-2, who was groomed by three individuals only. PC2 in this group, as in group H2, is correlated neither with age nor with dominance index.

According to Table 7, only in the male group did an enhanced number of "victories" in agonistic contacts significantly enhance the "winner's" chances of receiving grooming from the "defeated" animal. An increase in the number of "defeats," on the other hand, made the "loser" less attractive (insignificantly, though) as a passive grooming partner for the "winner." In heterosexual groups the reverse was the case (significant in females of group H1).

As Table 7 demonstrates, group M was the only one in which maternal kinship had no effect on grooming behavior.

Grooming and individual preferences.

Individual grooming preferences, which might be described as friendship, existed in all three groups. All the chi-squared values for the reduced matrices (after the exclusion of animals for which at least one expected frequency fell below 1) are highly significant ($P < 0.001$): 744.2 for group H1 ($df = 71$), 474.5 for group H2 ($df = 55$), and 246.8 for group M ($df = 41$). Tschuproff's T-coefficient of contingency for these matrices equals 0.38 and 0.58 (females only, 0.43 and 0.65) in groups H1 and H2, vs. 0.39 in group M. For unreduced matrices, Tschuproff's T-coeffi-

cient equals 0.39 and 0.41 (females only, 0.42 and 0.40), vs. 0.33, respectively. Thus, affiliative preferences were somewhat less marked in the male group than in heterosexual groups.

The differences between the male group and the two other groups are summarized in Table 11.

The extortion hypothesis. Do our data support the extortion hypothesis? If social position is evaluated by means of the dominance index, none of the groups shows a significant correlation between this measure and the coefficient of grooming status, no matter whether males are "excluded" from the bisexual groups or not (Tables 2–5). In group H1, the correlation is insignificant and negative ($r = -0.44$, $P < 0.10$), due to the high grooming performance of the alpha male (Butovskaya et al., 1994). The correlation, however, disappears when only females are considered. None of the three alpha males had a high grooming status. Their ranks on this measure were either low (group H1, 17th) or medium (group H2, 12th; group M, seventh). The same applies to alpha females in groups H1 (15th) and H2 (ninth). So none of our data directly support the extortion hypothesis. Some indirect evidence in favor of it may be obtained by considering age, but only in the male group, since in males age can be used as a predictor of status. The correlation between the coefficient of grooming status and age in group M is insignificant ($r = 0.57$, $P < 0.10$) (Table 5). In group H2, however, it is highly significant ($r = 0.59$, $P < 0.01$), regardless of the exclusion or nonexclusion of males; but age cannot be used to predict status in females (although these two variables are correlated in females of group H2). Also, grooming status

TABLE 11. Differences between the all-male group and the mixed sex groups

Parameter	Bisexual groups	All-male group
Social hierarchy	More linear	Less linear
Agonistic and affiliative activity of low-ranking animals toward higher-ranking ones	Lower	Higher
More variable aspect of grooming	Performance	Attractiveness
Positive correlation between received grooming and social status (or age)	Weaker	Stronger
Animal groomed by the largest number of partners	Female (rank varies)	Alpha male
Effect of maternal kinship on grooming behavior	Significant	Insignificant
Individual preferences	Stronger	Weaker

in this group is associated with age not so much because older females were groomed more often than the younger ones as because they groomed less. In group H1, the correlation is low and negative. So while the extortion hypothesis may be correct with respect to some groups of stumpails, it cannot be universally true for this species.

The structure of grooming relationships. The results of cluster analysis and nonmetric multidimensional scaling of grooming distances are represented in Figures 4–6. The analysis of the structure of affiliative relations demonstrates that although, as shown above, maternal kinship did influence grooming behavior in the bisexual groups, its effect was not strong. Some pairs of relatives did form stable grooming dyads (the alpha male C-1 and his sister C-2 in group H1, mother–daughter pairs M-1 and M-3, N-2 and N-3, S-1 and S-2 in group H2), but members of other pairs were far apart in the grooming space. On the other hand, some unrelated animals were linked by close friendly bonds, and none of the factors considered by us appear to be crucial for such contacts. Examples in group H1 are females E-1 (old, high ranking) and D-3 (young, low ranking), K-1 (young, high ranking) and 1 (medium aged, low ranking); in group H2, the young low-ranking male N-1 and the old high-ranking female R-1, as well as females X-1 (young, low ranking) and 2 (medium aged, medium ranking). The negative correlation between the amount of grooming and difference in age and dominance status is significant only in group H1, where age similarity is especially important for grooming relationships (Table 7). How-

ever, in all groups low-ranking individuals tend to be peripheral in the grooming space (Figs. 4–6).

In the heterosexual groups, the higher-ranking females were more active than the lower-ranking ones in half of the significantly asymmetric grooming dyads, and in half the relation was reverse; no regularity can be seen in the distribution of these animals' ages. In the male group, the more active groomers were younger and their dominance status was lower in five asymmetric dyads out of six, in keeping with the tendency described above.

The role of gender and sex ratio in grooming behavior and its interrelation with dominance and other factors

Much to our regret, it was impossible for us to compare an all-male group with an all-female one. We have serious doubts as to whether the latter could exist in stumpail macaques. Although, as in other matrilineal species (Hrdy, 1986), stumpail females select sexual partners and apparently define which of the immigrant males will remain in the group, they paradoxically display little if any ability to regulate their relationships in the absence of the alpha male, who performs the controlling function with enviable efficiency. In contrast to rhesus and long-tailed macaques, stumpail females never attempt to threaten or attack alpha males, whose intrusion in agonistic interactions between the females, mostly on the side of victims, is nearly always effective (Butovskaya, 1993). Moreover, we have witnessed two cases (in different groups) when the removal of the male for 2–3 days resulted in an out-

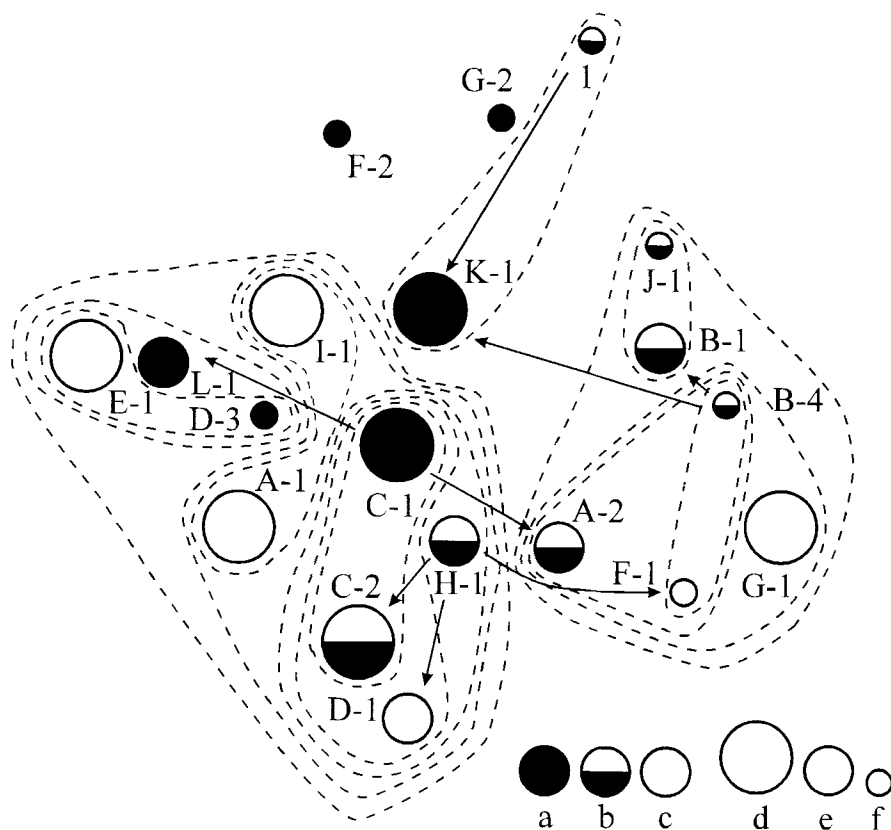


Fig. 4. Structure of grooming relations in group H1: results of cluster analysis and nonmetric multidimensional scaling of grooming distances. Clusters are shown by dashed lines. Arrows show the direction of greater activity in significantly asymmetrical dyads. Categories of individuals according to age: a, 7 years and younger; b, 8–10 years; c, 11 years and older. Categories of individuals according to dominance status: d, high; e, medium; f, low. C-1 is a male, others are females.

burst of severe interfemale violence which ceased immediately after the male had been returned. The same has been observed in groups of pigtail and longtailed macaques (Oswald and Erwin, 1976). Speaking of stump-tails as “nice” macaques (Moore, 1992), one should keep in mind that this epithet may not apply to an all-female group. The number of females that can be controlled by a single male is not known. The only thing one can say is that the disproportionately low male–female ratio in groups H1 and H2 did not appreciably decrease the alpha males’ efficiency as the controlling animals.

Apart from this common feature, the alpha males in the two heterosexual groups were very different in their behavior. The leader of the male group was closer to his counter-

part in group H1. Because of the dissimilarity of the alpha males, we are unable to make any generalizations concerning their behavior. Nevertheless, it is possible to claim that the normal strategy of low-ranking stump-tail males is to maintain relationships with senior individuals. This feature clearly distinguishes subordinate males from subordinate females, and this applies not only to members of the all-male group, but to the low-ranking male in group H2 as well, since he used the same strategy. It is in the all-male group that Seyfarth’s model of high-ranking animals receiving the most grooming worked best.

The frequency of agonistic behavior in the all-male group was higher than it was in heterosexual groups, mostly due to the

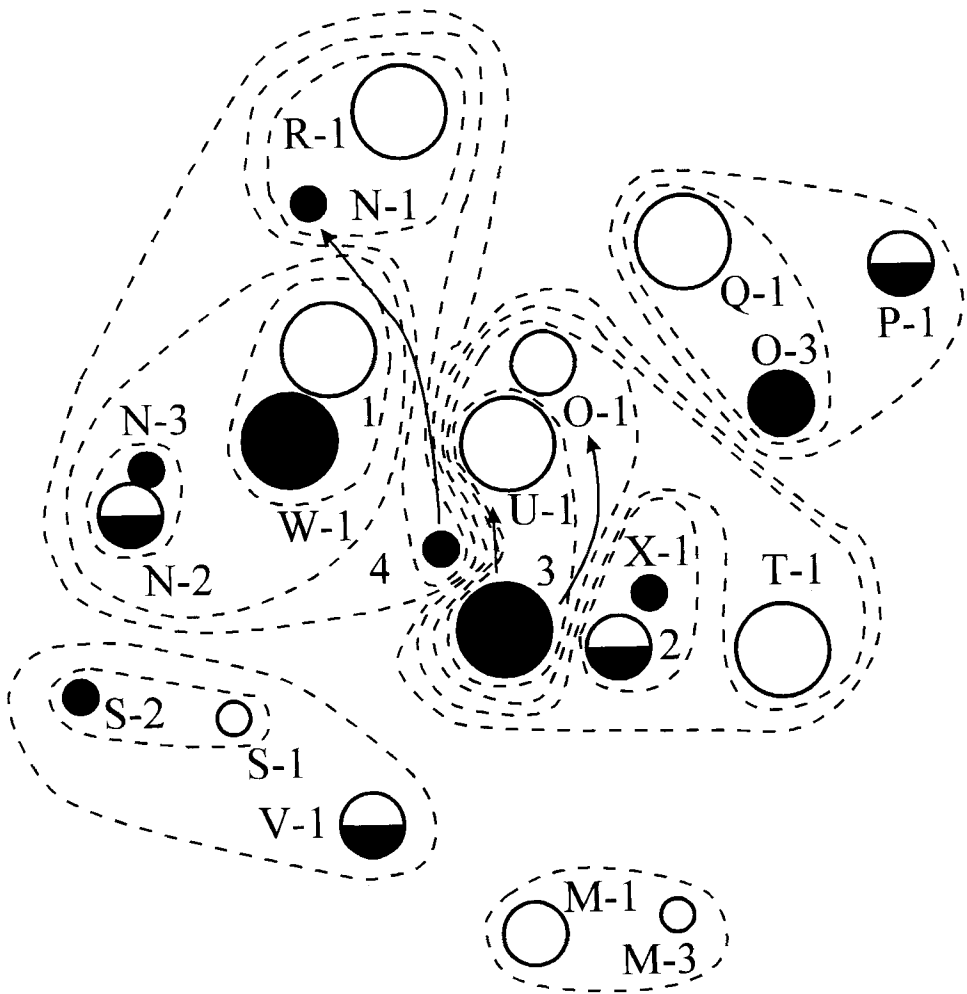


Fig. 5. Structure of grooming relations in group H2 (1 and N-1 are males, others are females). See Figure 4 for explanations.

greater involvement of low-ranking males, who, in this respect as well, were more active than low-ranking females. However, the occurrence of contact aggression in group M was lower, evidently because conflicts between males more often result in serious injuries than do those between females (Whitten and Smith, 1984; Ruehlmann et al., 1988).

We believe that these features of male behavior in stump-tail macaques may be related to dispersal patterns. As the data on Barbary and bonnet macaques (species apparently close to stump-tails in dominance

style) suggest, male migration rate in stump-tails may be low (Caldecott, 1986). The presence of a large number of males in the group might have favored the development of strategies aimed at establishing alliances with animals of a higher social position. Such strategies are probably part of the "soft" dominance style. Since status is not inherited in males, their active behavior, both agonistic and friendly, helps them maintain and enhance their position, which, as our results confirm, rises until a certain age and is known to decline afterward. When emigration is not a common option, it is especially

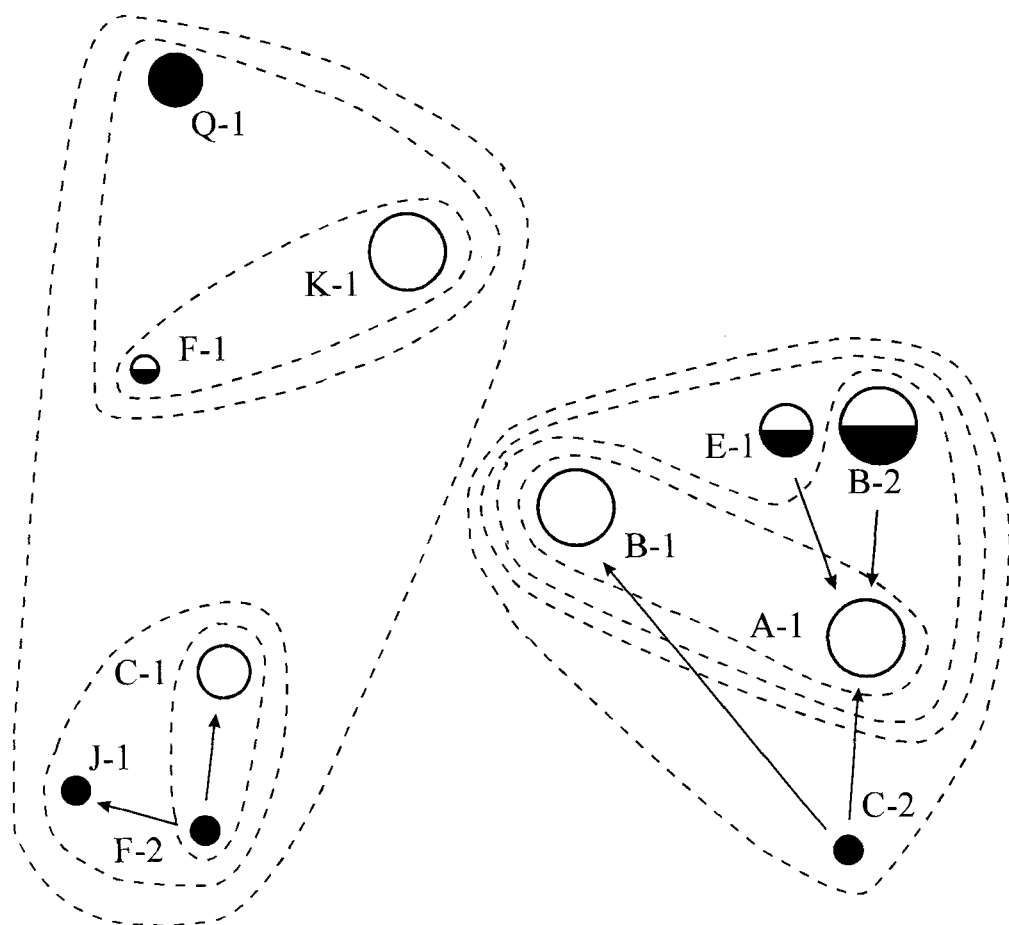


Fig. 6. Structure of grooming relations in group M. All animals are males. See Figure 4 for explanations.

profitable for males to establish a flexible network of social bonds. Because rank is liable to change, such behavior is hardly compatible with long-lasting individual preferences. Kinship was not found to exert any effect on the affiliative behavior in the male group, probably because all its members had grown up together and were very familiar with one another (see Santillan-Doherty et al., 1991, for the same result).

Females inherit their social ranks from their mothers, and there is little change in status after puberty. This, together with the presence of the male leaders, had probably made the social hierarchy in heterosexual groups more linear and apparently more sta-

ble. Low-ranking females, in contrast to their male counterparts, preferred not to pursue any active strategies (agonistic or peaceful) with respect to animals of a higher social status, either females or males, and kept a low profile. Generally, however, rather than being a means of enhancing or maintaining social position, grooming for the females seems to be a manifestation of individual preferences, which were more marked here than they were in the male group, in keeping with the results of other authors (de Waal, 1984; de Waal and Luttrell, 1986; Harcourt, 1987). A similar tendency has been observed in experimental play situations in humans (Murnighan, 1978). Strong

individual preferences seem to be the primary reason why stumptail females are unable to regulate relations between the matriline in the absence of the alpha male. The same may apply to pigtail and longtailed macaques (Oswald and Erwin, 1976).

The social functions of grooming in two heterosexual groups were different. In group H1, high-ranking individuals were actively engaged in establishing relations with their immediate subordinates (this probably accounted for the significant positive correlation between rank similarity and the intensity of grooming relationships, predicted by Seyfarth's model). This was especially typical of the alpha male, who performed more grooming than he received, just the opposite of what might be expected according to the extortion hypothesis. In group H2, the alpha male was much less active, and grooming performance in females showed a negative correlation with age regardless of dominance status (the same tendency has been registered in female Japanese monkeys; see Nakamichi, 1984). These differences are most likely due to individual characteristics of the animals.

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